Overstory dynamics as an indicator of ecosystem services from the understory vegetation in coniferous forests in Sweden

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Abstract

Understory vegetation is a wide and diverse part of the forest environment, which provides a lot of information about the forest, its condition and ecosystem services. Understory vegetation is affected and moulded by the species composition and density of the overstory, which changes growth conditions and productivity in the lower layers during the whole rotation period.

National Forest Inventories (NFI) supply long term time series of forest conditions. Recently NFIs also widened the scope to include other ecosystem variables, e.g. different biodiversity components, carbon sequestration and deadwood occurrence. Hence, there is a great opportunity, with data from this source, to analyse the correlation between understory and overstory vegetation, and make inferences on the relationship between these selected features and their influence on ecosystem services.

The aim of this thesis is to study understory ecosystem services in coniferous stands in the boreal and hemi-boreal regions of Sweden by analysing correlations between understory and overstory vegetation. The data for this study was acquired from the Swedish NFI. Interest of this research is narrowed to spruce and pine dominated stands, which are selected from among thousands of available study plots in the NFI database. The plots are sorted depending on dominant tree species and age into species specific chronosequences. Furthermore there is also a latitude gradient criterion – analyses were performed separately for 5 different region of Sweden.

In this study, by analysing almost 16 000 sample plots, the following ecosystem services were researched:

1) supporting ecosystem services (biodiversity based on vascular plant species number in the field-layer and game potential based on vascular plant cover in the field-layer)
2) provisioning ecosystem service (berry production based on bilberry and cowberry cover)

There are several significant differences in occurrence of the studied ecosystem services depending on the overstory. Spruce dominated stands have a higher biodiversity than pine stand in most of Sweden (regions 1-4; in all age classes), but the situation inverts in the most southern region (5). The highest game potential occurs in northern Sweden in spruce stands, and in southern Sweden in pine stands. The bilberry production rises proportionally with the age, irrespective of stand type. The highest cowberry production occurs in pine dominated stands, independently of region and age class. Differences between age classes in output of ecosystem services are much smaller in northern Sweden than in the southern part of the country.

Keywords: berry production, biodiversity, ecosystem services, game potential, overstory vegetation dynamics, *Picea abies*, *Pinus sylvestris*, understory vegetation, *Vaccinium myrtillus, Vaccinium vitis-idaea,*

Streszczenie

Warstwa podszytu i runa leśnego to ważna część leśnego środowiska, na podstawie której można czerpać wiele informacji na temat lasu, jak i usług ekosystemowych. Rozwój podszytu i runa leśnego jest kształtowany przez gatunki roślin w nim występujące, oraz przez warstwę koron drzew, które wpływają na rozwój roślin i wegetację, podczas całego okresu odnowieniowego.

Szwedzka Państwowa Inwentaryzacja Leśna (NFI) pozyskuje długoterminowe dane na temat stanu lasów. Ostatnimi czasy NFI poszerzyła obszar zbieranych danych, które obecnie zawierają więcej informacji na temat innych cech ekosystemu, tj. akumulacja węgla, czy obecność martwego drewna. W związku z powyższym na podstawie analizy danych pochodzących z NFI istnieje możliwość zbadania korelacji pomiędzy rozwojem warstw runa leśnego, podszytu i koron drzew oraz wnioskowania powiązań między nimi oraz ich wpływu na usługi ekosystemowe.

Celem tej pracy jest zbadanie usług ekosystemowych runa leśnego w borealnych oraz hemiborealnych regionach Szwecji, poprzez zbadanie korelacji rozwoju warstw dolnych oraz koron drzew. Dane wykorzystane do badań zostały zebrane podczas Szwedzkiej Państwowej Inwentaryzacji Leśnej (NFI). W pracy tej skupiono się na drzewostanach sosnowych i świerkowych, które wyselekcjonowano według specjalnej formuły z pośród tysięcy dostępnych powierzchni próbnych. Powierzchnie te zostały pogrupowane w zależności od dominującego gatunku drzewa oraz klasy wieku drzewostanu. Ponadto jednym z kryteriów była szerokość geograficzna – analizy zostały przeprowadzone osobno dla 5 różnych regionów Szwecji.

W tej pracy, na podstawie analizy prawie 16 tysięcy powierzchni próbnych, zostały zbadane następujące usługi ekosystemowe:

1) Usługi przestrzeni życiowej (bioróżnorodność zbadana na podstawie liczby gatunków roślin naczyniowych występujących w warstwie runa oraz potencjał do polowań zbadany na podstawie procentowego pokrycia powierzchni runa przez rośliny naczyniowe
2) Usługi produkcyjne (produkcja jagód na podstawie procentowego pokrycia powierzchni przez gatunki *Vaccinium myrtillus L.* oraz *Vaccinium vitis-idaea* L.

W tej pracy badawczej zaobserwowano wyraźne trendy w występowaniu usług ekosystemowych zależnych od warstwy koron drzew. Wyższy wskaźnik bioróżnorodności wykryto w drzewostanie świerkowym, niż w sosnowym w regionach od 1 do 4 (we wszystkich klasach wieku). Sytuacja jest zupełnie odwrotna tylko w przypadku najbardziej wysuniętego na południe regionu 5. Wyższy potencjał do polowań wykryto w drzewostanach świerkowych w północnej cześci Szwecji, podczas gdy w południowej wyższy wskaźnik zaobserwowano w drzewostanach sosnowych. Wskaźnik produkcji jagód dla gatunku *Vaccinium myrtillus L.* rośnie wprost proporcjonalnie z klasą wieku, bez względu na typ drzewostanu. Wyższa produkcja jagód dla gatunku *Vaccinium vitis-idaea L.* występuje w drzewostanach sosnowych, niż świerkowych – bez względu na region i klasę wieku. Różnice pomiędzy wynikami badanymi w odniesieniu do klas wieku dla usług ekosystemowych są dużo mniejsze dla powierzchni próbnych w północnej Szwecji niż w południwej.

Słowa kluczowe: bioróżnorodność, dynamika rozwoju warstwy koron drzew, rozwój podszytu, usługi ekosystemowe, *Picea abies*, *Pinus sylvestris*, potencjał do polowania, produkcja jagód, *Vaccinium myrtillus, Vaccinium vitis-idaea*

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Introduction

Ecosystem services

Every human being depends (directly or indirectly) on the Globe's ecosystems – the various communities of living organisms in connection with the non-living components of their environment. It happens, because we use the benefits provided by ecosystems, which are necessary for our existence. The name of these benefits is ecosystem services. The importance of forests has mostly been recognized through goods that it provides, such as timber, fuelwood and other non-timber forest products, but nowadays the importance of other ecosystem services, which are crucial for the cycle of life, is increasingly stressed (Nodvin, 2008). A definition of ecosystem services says, that they are the conditions and processes through which ecosystems, and the species that make them up, sustain and fulfil human life (Daily, 1997). They maintain biodiversity and the production of ecosystem goods, such as forage, timber, biomass fuels, natural fiber, and many pharmaceuticals, industrial products, and their precursors. In addition to the production of goods, ecosystem services are the actual life-support functions, such as cleansing and renewal of the environment, and they promote many intangible aesthetic and cultural benefits as well. Ecosystem services can be divided into four main categories, which are significant for human well-being (Zakri & Watson, 2005):

1) Provisioning services – material or energy outputs from ecosystems (as food, water and other resources),
2) Regulating services – the benefits obtained from the regulation of ecosystems processes (as air quality, climate, water, erosion regulations),
3) Habitat or supporting services – services necessary for the production of all other ecosystem services (as soil formation, photosynthesis, primary production),
4) Cultural services – nonmaterial benefits obtained through spiritual enrichment, cognitive development, recreation (as cultural diversity, spiritual, religious and educational values).

Different branches of industry are focused on differentiated activities. To improve ecosystem output, humans can affect the balance between different goods and services. To facilitate this, it is really important to have the possibility to estimate the occurrence and frequency of these ecosystem services under different management regimes. With this knowledge we can improve the environmental outputs and uphold sustainable and rational use of ecosystem services.

Forests provide many different types of ecosystem services. The trees provide timber and fuelwood, while shrubs provide non-timber products like berries. All these outputs are classified as provisioning services. Additionally, forests are really important by their influence on climate, quality of air and erosion control. Hence, forests play a significant role of the sustainable development of our planet through regulating ecosystem services (Zakri &

Watson, 2005). Forests are also home for biodiversity of plant and animal species – i.e. they create habitat and supporting services, which are the foundation for other ecosystem services. Last, but not least, cultural services, which since prehistoric period inspire, delight and develop spiritual and educational experiences of human beings. The most common cultural ecosystem services are: recreation, tourism, cultural inspiration, relaxation and health (Elmqvist, 2015). While all of these ecosystem services are important, this study is mainly about provisioning (berry production) and supporting (biodiversity and game potential) ecosystem services.

Linkages between biodiversity and ecosystem services

Definition of biodiversity describes it as diversity among and within plant and animal species in an environment. There is a positive relationship between the majority of biodiversity attributes and ecosystem services. By increases in community and habitat area there is an observed improvement of the services of water quality regulation, water flow regulation, mass flow regulation and landscape aesthetics. Atmospheric regulation, pest regulation and pollination display a predominantly positive relationship in connection with species richness and diversity. Species richness has been found beneficial for timber production and freshwater fishing, while species abundance was important for pest regulation, pollination and recreation (Gamfeldt et al., 2013; Harrison et al., 2014). These relations between biodiversity and ES are highly complex and service dependent, but the positive effects of biodiversity dominate.

Figure 1. Vaccinium myrtillus L. in pine stand (photo: Daniel Boczniewicz).

Bilberry and cowberry

Bilberry *(Vaccinium myrtillus L.)* and cowberry *(Vaccinium vitis-idaea L.)* are the most common forest berry species in Scandinavia (Turtiainen, 2015). Bilberry and cowberry occur on a wide range of different site and land types, mostly in coniferous ecosystems (Figure 1. and 2.). Due to this they are distributed almost across all of Europe and northern Asia (Ritchie, 1955). Bilberry is most abundant in heath forests of medium site fertility, while cowberry is adapted to drier growing conditions and is most typical in light pine-dominated heath forests (Raatikainen et al., 1984). Both these species are economically important. According to calculations, annual bilberry yields in Finland vary from 92 to 312 million kg, while cowberry yields vary from 129 to 386 million kg (Turtiainen et al. 2011). Respectively for Sweden bilberry yields vary between 219 and 307 million kg, while cowberry yields vary between 142 and 168 million kg per year (Kardell, 1980). Even if numbers are high, it is just 5 to 10% of the total yield of wild berries, which is utilized (Turtiainen et al. 2011). Berry pickers are collecting them for their household´s use and for sale. That makes berry picking, besides being an recreational activity, an important additional source of income, especially in regions with high unemployment rates (Kangas, 2000). Except human's use of berries these shrubs are also a significant part of forest ecosystems as both leaves, stems and berries are important food sources for forest animals (e.g. capercaillie, *Tetrao urogallus*) (Selås, 2001).

Figure 2. Vaccinium vitis-idaea L. in pine stand (photo: Daniel Boczniewicz).

Game potential

Sweden is a country with great game potential. Due to long hunting traditions there are a lot of different types of hunting, for example: traditional moose hunting, hunting with a pointing dog, beaver hunting and the winter hunts for grouse and black grouse. There is great variety of wildlife and game animals, not found outside Scandinavia (Mattsson, 1990). The most popular game species in Sweden are: moose (*Alces alces)*, red deer (*Cervus elaphus)*, roe deer (*Capreolus capreolus)*, beaver *(Castor fiber)*, alpine hare *(Lepus timidus)*, capercaillie *(Tetrao urogallus)*, and black grouse *(Lyrulus tetrix)* (Kagervall, 2014). Vascular plant species in the field-layer form the basic sources of food for most of those species. Game forage potential is a supporting ecosystem service and creates preconditions for different important services, i.e. hunting as cultural ecosystem service and game as provisioning ecosystem service (Gamfeldt et al., 2013).

Overstory-understory interactions

The influence of tree species on the understory vegetation is very strong. The forest type has crucial impact for forest floor vegetation. The dynamics of overstory vegetation shape the understory development. For example the pine biomass is positively related to occurrence of bilberry shrubs and their production (Gamfeldt et al., 2013). The really important aspect, which also shapes understory and overstory relationships is the response of *Vaccinium* shrubs to disturbances. After fire, understory vegetation abundance and diversity increase rapidly. The fast growing and easily dispersed tree species colonize available growing space and form single-storied canopies, allowing the establishment of understories. When the canopy breaks down, shade tolerant tree species occupy gaps and form uneven-aged stands (Chen & Hart, 2006). The process of stand dynamics can be grouped in four development stages: 1) stand initiations; 2) stem exclusion; 3) canopy transition; 4) gap dynamics (Chen & Popadiouk, 2002). A big advantage of *Vaccinium* species, which causes good performance during stand initiation stage after intense fire, is that *Vaccinium* shrubs are rooted deep in the ground and therefore are more resilient to disturbance than herbaceous species with reproductive tissues in the humus layer. Therefore *Vaccinium* species are present during the first stage of forest development and increase their cover proportionally to increase of stand age (Chen & Hart, 2006).

The most common disturbance in Swedish forests is clear-felling, which is an inherent part of nowadays forestry. It has a negative influence on *Vaccinium* shrubs – the occurrence of shrubs decreases linearly with increasing logging intensity (Bergstedt & Milberg, 2001). These species' sensitivity to clear cutting has also been shown by Kardell (1980). In addition to the strong influence of the overstory on understory vegetation there is also a strong impact in the opposite direction, i.e. the initial success of seedlings (including regeneration of dominant tree species), which will occupy overstory is dependent of competitive interactions within the floor layer. Many tall-growing woody understory species can compete with tree seedlings for both light and nutrients which will influence the development of the tree layer.

The forest management treatments can also show how understory and overstory interact with each other. After heavy thinning in understory we can observe biomass increase of overstory biomass trees. And after cutting trees from overstory we can observe that understory species are filling the freed space (Abella et al., 2012). Summarizing, there is a both-sided dependency between floor layer, understory and overstory and every layer depends on another one (Jameson, 1967; George and Bazzaz, 2003; Abella et al., 2012).

Pine and spruce

Scots pine (*Pinus sylvestris)* and Norway spruce (*Picea abies*) (hereafter pine and spruce) are occurring all over Sweden and are the dominant forest tree species. Pine is more competitive on relatively poor and dry sites, comparing to spruce. As a pioneer species it occurs naturally on open areas (especially after clear-felling), fire and different disturbances. Spruce prefers richer soils with a good supply of water. It is a late succession species, regenerates naturally in the understory (although it´s mostly planted on clear-cuts in commercial forestry); after this it may dominate the natural succession for longer periods in the absence of disturbance (Zhang, 2012; McCarthy, 2001). These two species are favoured by Swedish private forest owners and forestry industries for management due to high productivity and easy management. The tradition aspect and promotion of relevant policies in Sweden for decades also influenced this situation (Barklund, 2009). The total standing volume in Swedish forests consists of 42% spruce and 39% pine (Swedish Forest Agency, 2011). The dominating management principle for those two coniferous species in Swedish forestry is monoculture plantation (often with a small share of deciduous broadleaved species) with clear-felling. Rotation for spruce can be much shorter comparing to pine (especially in connection to beneficial temperature, site index or type of soil). What is also in favour for spruce – there are not so high requirements of the timber quality in sawmills as for pine, so there is a lower risk for forest owners, if failures in management occur. The most common planting density currently used in Swedish forestry is 2500 trees per hectare, which give us an initial spacing 2m x 2m (Zhang, 2012).

Geography and climate of Sweden

Sweden is situated in Northern Europe between latitudes 55° and 70° N and mostly between longitudes 11° and 25° E. It forms the eastern part of the Scandinavian Peninsula. The total area is 447 429 km^2 with 280 730 km^2 of forest (The World Bank Data, 2015). Due to this we can observe varied average duration of the growing season from below 120 days to above 240 days per year (Wastenson and Nilsson, 1990).

Swedish National Forest Inventory

The National Forest Inventory (NFI) in Sweden is a programme with the main goal to monitor woodland and trees on a national level. It provides an extensive and unique record of key information about the forests (Tomppo et al., 2010); information, which can become basis for biodiversity assessment and reporting, as ground vegetation, dead wood, special indicators, forest continuity, etc. (Stokland, 2003). The first Swedish NFI took place in the 1920s and it was initiated to counteract decreasing growing stock and the lack of regeneration after selective logging operations by collecting and tracking data connected with those actions. At that time the main focus was based on information about forest growth and productivity (Tomppo et al., 2011). Idea of collecting data via NFI has evolved to these days to become more detailed and extensive – from solely estimates of timber resources to environmental monitoring. Also methods and design changed over time from county wise strip survey sampling to cluster sampling for the whole country. The contemporary type of Swedish NFI was begun in 1983 and it is performed by the Swedish University of Agricultural Sciences.

The NFI's data and their analyses can have significant potential in research (Fridman et al., 2014). Especially, there are great opportunities to estimate and define important ecosystem services. The objective of this paper is to increase our knowledge about the output of different ecosystem services, depending on forest structure and management models. There is an opportunity to do this by analysing data from the National Forest Inventories.

Hypotheses

In the study the following hypotheses will be tested:

1. *The berry production increases with stand age.*
   According Kardell (1980) and Hedwall et al. (2013) there is positive relation between berry production and stand age. Hence I expected the berry production to be higher in old stands than in young stands.
2. *The berry production is higher in pine dominated stands in comparison with spruce dominated stands.*
   According to the literature there is a positive correlation between bilberry and cowberry production and pine biomass, and a negative correlation with spruce biomass (Gamfeld et al., 2013, Miina et al., 2009). Because of this I expected pine dominance to be beneficial over spruce dominance for berry production.
3. *The biodiversity decreases with stand age.*
   In younger stands there should be higher diversity of vascular plant species due to better light and nutrient availability. This trend should decrease with age, due to effect of competition and limited resources (Chen & Hart, 2006).
4. *The game production potential is higher in younger and older stands in comparison with middle aged ones.*
   The young and old age classes should contain higher vascular plant cover and be more open for animals – especially ungulates.

5. *The differences between age classes in output of ecosystem services will be smaller in northern Sweden than in the south.*
   Stand dynamics are slower and extended in time in northern Sweden, due to lower soil fertility, stricter climate condition and shorter vegetation period, comparing to southern Sweden. This leads to smaller variation in overstory influence over time and to less dense canopies.

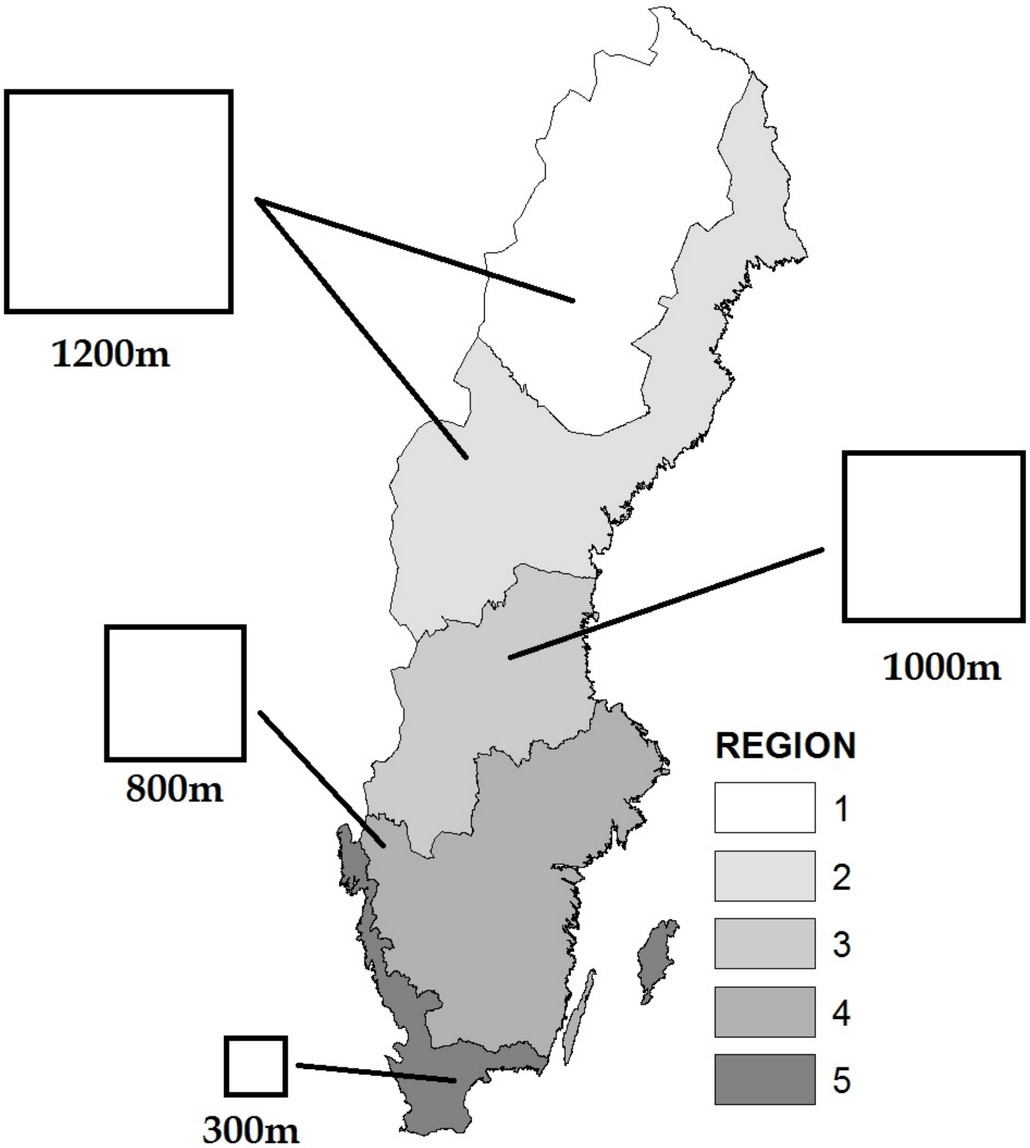

Figure 3. Regional division and size variation for permanent clusters. Redrawn after: Tomppo et al. 2010.

Materials and methods

Scheme of work

This paper is based on data from the Swedish NFI, which were used to investigate understory ecosystem services in coniferous stands. Four different indicators of different ecosystem services were used:

1) Biodiversity indicator (based on vascular plant species number in the field-layer) as a supporting ecosystem service,
2) Game potential indicator (based on total vascular plant species cover in the field-layer) as a supporting ecosystem service,
3) Bilberry production indicator (based on bilberry cover) as provisioning ecosystem service,
4) Cowberry production indicator (based on cowberry cover) as provisioning ecosystem service.

To examine results for the biodiversity indicator, the analyses were based on 15 642 sample plots (Table 2.) and 199 different vascular plant species (Table 4.). For the different indicators of game potential, bilberry and cowberry production, the analyses were based on 7 790 sample plots (Table 3.). The plots were grouped according to:

a) Region (Figure 3.)
b) Stand type – pine or spruce dominated stand (share of dominant tree species greater than or equal to 70%)
c) Age class – there are six age classes (Table 1.)

All calculation and analyses were made in Excel 2014 and R (R Core Team, 2015). In R the following packages were used: dplyr, lsmeans, ggplot and ggplot2. The final graphs were made in R Studio.

Swedish NFI – obtaining data

The Swedish NFI is using circular plots, which are arranged in quadratic clusters. The size of these clusters and the distance between them varies between different parts of the country: smaller clusters and distance in southern Sweden than in northern Sweden. The Swedish NFI is based on two types of clusters: temporary and permanent ones (Figure 4.). Temporary clusters are surveyed only once, while permanent clusters are resurveyed regularly in intervals of 5-10 years depending on surveyed variable. On the permanent clusters tree data is collected on plots with 10m radius. (Tomppo et al., 2010). In this study only permanent clusters with detailed vegetation data are used. The radii for the vegetation plots were 5,64m with the same centre as the 10m plot.

This study uses data from 2004 till 2013. It means, that they come from the eight (2003-2012) and the ninth (2013) Swedish National Inventories.

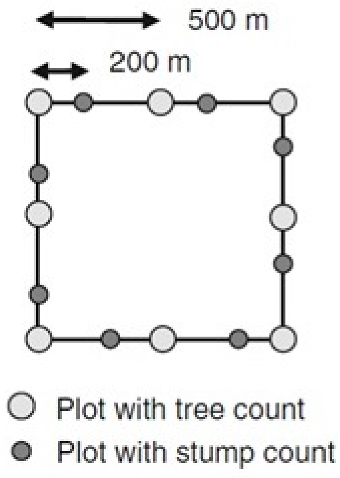

Figure 4. Examples of plot configuration within permanent clusters from region 3. Only on light grey plots tree count is performed while stump inventory is performed on dark grey plots. Source: Tomppo et al. 2010

Table 1. Age classes distribution.

age class	age (years)
I	< 10
II	10 –19
III	20 – 39
IV	40 – 69
V	70 – 99
VI	≥ 100

Table 2. Distribution of plots used to estimate vascular plant species number in the field-layer as an indicator of biodiversity dependent on region, stand type and age class.

total plots number : 15 642

region	1											
plots	1432											
tree species	pine						spruce					
plots	580						852					
age class	I	II	III	IV	V	VI	I	II	III	IV	V	VI
plots	22	41	110	179	91	137	72	64	116	150	86	364

region	2											
plots	4290											
tree species	pine						spruce					
plots	1414						2876					
age class	I	II	III	IV	V	VI	I	II	III	IV	V	VI
plots	77	120	382	297	166	372	410	264	490	518	362	832

region	3											
plots	3315											
tree species	pine						spruce					
plots	1208						2107					
age class	I	II	III	IV	V	VI	I	II	III	IV	V	VI
plots	63	129	345	262	99	310	327	209	455	505	278	333

region	4											
plots	5324											
tree species	pine						spruce					
plots	1257						4067					
age class	I	II	III	IV	V	VI	I	II	III	IV	V	VI
plots	103	94	301	279	235	245	597	447	869	1000	746	408

region	5											
plots	1281											
tree species	pine						spruce					
plots	205						1076					
age class	I	II	III	IV	V	VI	I	II	III	IV	V	VI
plots	19	13	29	36	53	55	142	85	233	299	222	95

Table 3. Distribution of plots used to estimate cover of vascular plants, bilberry and cowberry dependent on region, stand type and age class.

total plots number : 7 790

region	1											
plots	720											
tree species	Pine						spruce					
plots	285						435					
age class	I	II	III	IV	V	VI	I	II	III	IV	V	VI
plots	13	21	55	81	50	65	38	36	58	74	45	184

region	2											
plots	2135											
tree species	Pine						spruce					
plots	712						1423					
age class	I	II	III	IV	V	VI	I	II	III	IV	V	VI
plots	42	73	206	130	85	176	225	127	264	233	181	393

region	3											
plots	1647											
tree species	Pine						spruce					
plots	604						1043					
age class	I	II	III	IV	V	VI	I	II	III	IV	V	VI
plots	36	74	177	115	44	158	167	101	237	234	135	169

region	4											
plots	2649											
tree species	Pine						spruce					
plots	616						2033					
age class	I	II	III	IV	V	VI	I	II	III	IV	V	VI
plots	63	49	146	125	109	124	310	217	452	495	367	192

region	5											
plots	639											
tree species	Pine						spruce					
plots	97						542					
age class	I	II	III	IV	V	VI	I	II	III	IV	V	VI
plots	8	7	13	22	20	27	77	44	115	147	106	53

Table 4. List of all vascular plant species in the field-layer (199) researched in this study.

Achillea millefolium	*Cirsium palustre*	*Geranium sylvaticum*
Achillea ptarmica	*Cirsium vulgare*	*Geum rivale*
Aconitum lycoctonum	*Convallaria majalis*	*Geum urbanum*
Actaea spicata & erythrocarpa	*Corallorhiza trifida*	*Goodyera repens*
Aegopodium podagraria	*Cornus suecica*	*Gymnocarpium dryopteris*
Agrostis capillaris	*Corydalis spp*	*Hepatica nobilis*
Allium ursinum	*Corylus avellana*	*Huperzia selago*
Andromeda polifolia	*Crataegus spp*	*Hypericum spp*
Anemone nemorosa	*Crepis paludosa*	*Hypochoeris maculate*
Anemone ranunculoides	*Dactylorhiza maculata*	*Juncus conglomeratus/effusus*
Angelica sylvestris	*Daphne mezereum*	*Juncus filiformis*
Antennaria dioica	*Dentaria bulbifera*	*Juniperus communis*
Anthoxanthum odoratum	*Deschampsia cespitosa*	*Lamiastrum galeobdolon*
Anthriscus sylvestris	*Deschampsia flexuosa*	*Lathyrus linifolius*
Arctostaphylos uva-ursi	*Diphasiastrum complanatum*	*Lathyrus vernus*
Arnica montana	*Drosera spp*	*Ledum palustre*
Artemisia vulgaris	*Dryopteris carthusiana/dilatata*	*Leucanthemum vulgare*
Athyrium filix-femina & distentifolium	*Dryopteris filix-mas*	*Linnaea borealis*
Betula nana	*Empetrum nigrum*	*Listera cordata*
Bistorta vivipara	*Epilobium angustifolium*	*Listera ovata*
Calamagrostis arundinacea	*Epilobium montanum*	*Lonicera xylosteum*
Calamagrostis canescens/purpurea	*Equisetum arvense*	*Lotus corniculatus*
Calla palustris	*Equisetum fluviatile*	*Lupinus polyphyllus*
Calluna vulgaris	*Equisetum hyemale*	*Luzula campestris*
Caltha palustris	*Equisetum palustre*	*Luzula multiflora*
Carex chordorrhiza	*Equisetum pratense*	*Luzula pilosa*
Carex digitata	*Equisetum sylvaticum*	*Lycopodium annotinum*
Carex echinata	*Erica tetralix*	*Lycopodium clavatum*
Carex flava agg.	*Eriophorum angustifolium*	*Lysimachia thyrsiflora*
Carex globularis	*Eriophorum vaginatum*	*Lysimachia vulgaris*
Carex lasiocarpa	*Euphrasia_spp*	*Maianthemum bifolium*
Carex magellanica/limosa	*Filipendula ulmaria*	*Matricaria perforate*
Carex panicea/vaginata	*Filipendula vulgaris*	*Matteuccia struthiopteris*
Carex pauciflora	*Fragaria spp*	*Melampyrum pratense*
Carex rostrata	*Frangula alnus*	*Melampyrum sylvaticum*
Chrysosplenium spp.	*Gagea spp*	*Melica nutans*
Cicerbita alpina	*Galeopsis spp*	*Menyanthes trifoliate*
Cirsium arvense	*Galium boreale*	*Mercurialis perennis*
Cirsium helenioides	*Galium odoratum*	*Milium effusum*
	Galium verum	*Moehringia trinervia*

Molinia caerulea
Moneses uniflora
Mycelis muralis
Myrica gale
Nardus stricta
Narthecium ossifragum
Orthilia secunda
Oxalis acetosella
Paris quadrifolia
Parnassia palustris
Pedicularis palustris
Pedicularis sceptrum-carolinum
Petasites frigidus
Peucedanum palustre
Phegopteris connectilis
Phragmites australis
Pinguicula spp
Plantago major
Platatanthera spp
Poa nemoralis
Polygonatum spp
Polypodium vulgare
Potentilla anserine
Potentilla erecta
Potentilla palustris
Primula veris
Prunus spinosa
Pteridium aquilinum
Pulmonaria spp
Ranunculus ficaria
Rhynchospora alba
Ribes alpinum
Ribes nigrum
Ribes spicatum
Rubus arcticus
Rubus chamaemorus
Rubus idaeus
Rubus saxatilis
Rumex acetosa
Rumex acetosella
Sambuccus spp
Sanicula europaea

Saussurea alpina
Saxifraga granulata
Scheuchzeria palustris
Scirpus sylvaticus
Scrophularia nodosa
Selaginella selaginoides
Silene dioica
Solidago virgaurea
Stachys sylvatica
Stellaria graminea
Stellaria holostea
Stellaria nemorum
Succisa pratensis
Tanacetum vulgare
Thelypteris palustris
Tofieldia pusilla
Trichophorum alpinum
Trichophorum cespitosum
Trientalis europaea
Trifolium medium
Trifolium pratense
Trifolium repens
Trollius europaeus
Tussilago farfara
Typha spp
Urtica dioica
Vaccinium myrtillus
Vaccinium oxycoccus & microcarpum
Vaccinium uliginosum
Vaccinium vitis-idaea
Valeriana spp
Veronica chamaedrys
Veronica officinalis
Viburnum opulus
Viola mirabilis
Viola palustris/epipsila
Viola riviniana/reichenbachiana
Viola tricolor/arvensis

Results

Biodiversity indicator (based on the vascular plant species number in the field-layer)

There is a pattern, which shows that there is a higher biodiversity in spruce dominated stands than in pine stands in most of Sweden (regions 1-4; in all age classes). The situation is invert just in the very south (region 5), where the higher biodiversity occurs in pine dominated stands, comparing to spruce (in all age classes) (Figure 5.).

Analysing age classes, the highest diversity occurs in the younger stands. The peak differs a bit between regions and tree species from class 1st to 3rd (there is a pattern, which shows that classes 2nd and 3rd usually are in top 3 classes with highest biodiversity indicators). The trend is also less pronounced in spruce, than in pine stands (Figure 6.).

Game potential (based on vascular plant cover in % in the field-layer)

In northern Sweden a higher game potential occurs in spruce dominated stands (region 1). When moving to the south the situation changes – the game potential is high as well in spruce as in pine dominated stands (region 2-3). But in the southern part of Sweden (regions 4-5) there is significantly better game potential in pine dominated stand (Figure 7.).

From region 3 and southwards there is a clear trend in spruce stands. The highest game potential occurs in the younger age classes (1st and 2nd) and after this peak, there is very visible decline in 3rd class. In the older age classes the game potential seems to be much lower than in the younger ones (Figure 8.).

Bilberry production (based on bilberry cover in %)

In northern Sweden the higher bilberry production occurs in spruce dominated stands (region 1). The situation changes, when moving to the southern part of Sweden – there is a significantly higher bilberry production in pine dominated stands in regions 3-5.

There is a clear general north-south gradient in spruce stands, which shows that the best bilberry production occurs in 1st (most northern) region in Sweden and it declines proportionally with fall of latitude, with the lowest production in the 5th region (the most southern) (Figure 9.).

Independently of stand type, there is a pattern, which shows that bilberry production rises proportionally with the age classes – the best production occurs in the oldest classes (5th and 6th) (Figure 10.).

Cowberry production (based on cowberry cover in %)

Higher cowberry production occurs in pine dominated stands, than in spruce stands – independent of region and age class (Figure 11.).

Analysing age classes, we can observe that usually the cowberry production increases with age class, especially for region 1-3 (classes 5th and 6th is usually in top 3 classes with highest cowberry production) (Figure 12.).

The highest cowberry production is observed in the northern part of Sweden and the lowest in the most southern part. Hence, there is a pattern, which shows, that production decreases proportionally with decreasing latitude.

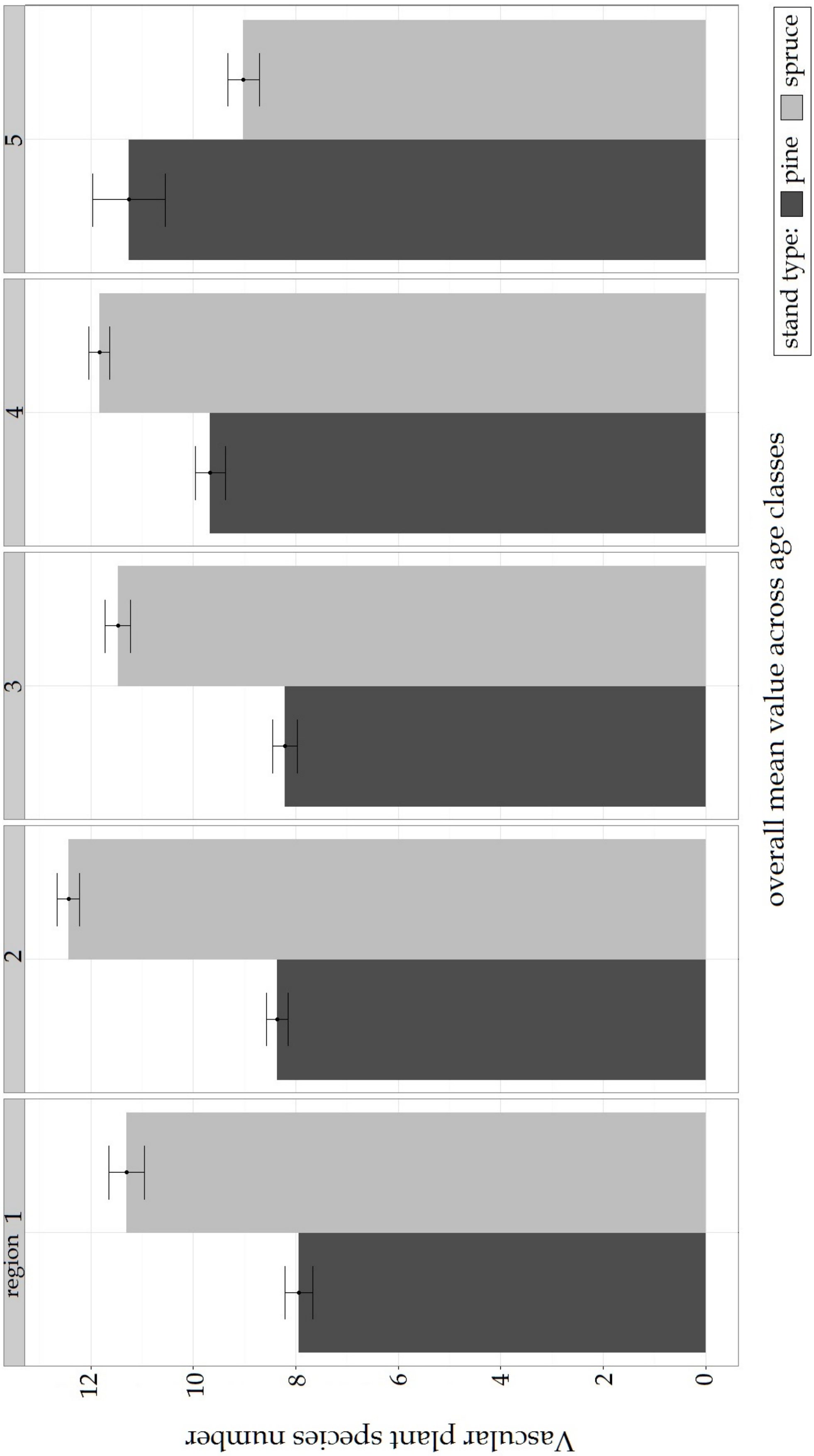

Figure 5. Overall mean values (across age classes) for vascular plant species number in the field-layer as an indicator of biodiversity dependent on stand type and region (Figure 3.) with 95% confidence intervals.

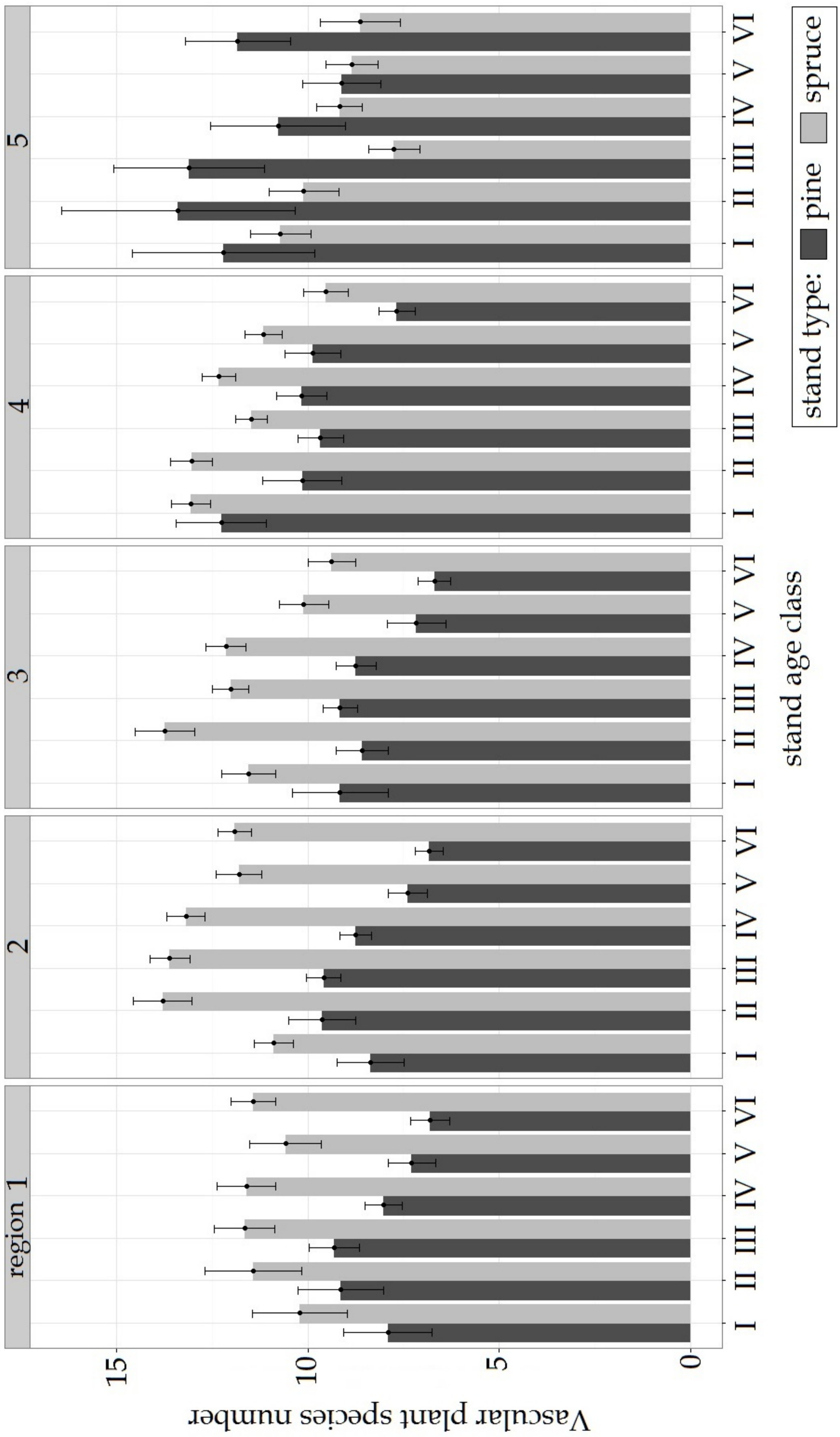

Figure 6. Vascular plant species number in the field-layer as an indicator of biodiversity dependent on stand type, age class (Table 1.) and (Figure 3.) with 95% confidence intervals.

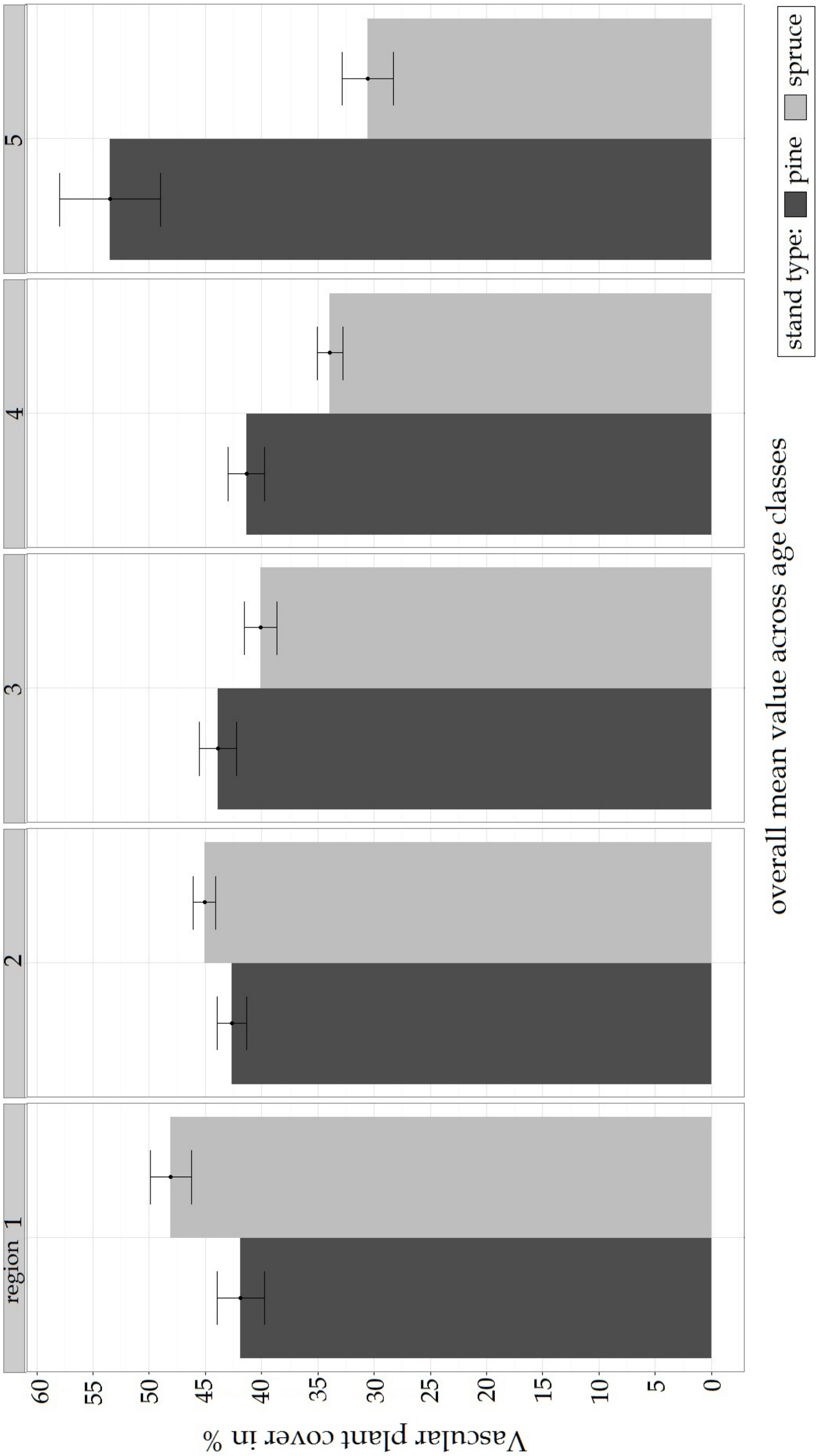

Figure 7. Overall mean values (across age classes) for vascular plant cover in % in the field-layer as an indicator of game potential dependent on stand type and region (Figure 3.) with 95% confidence intervals.

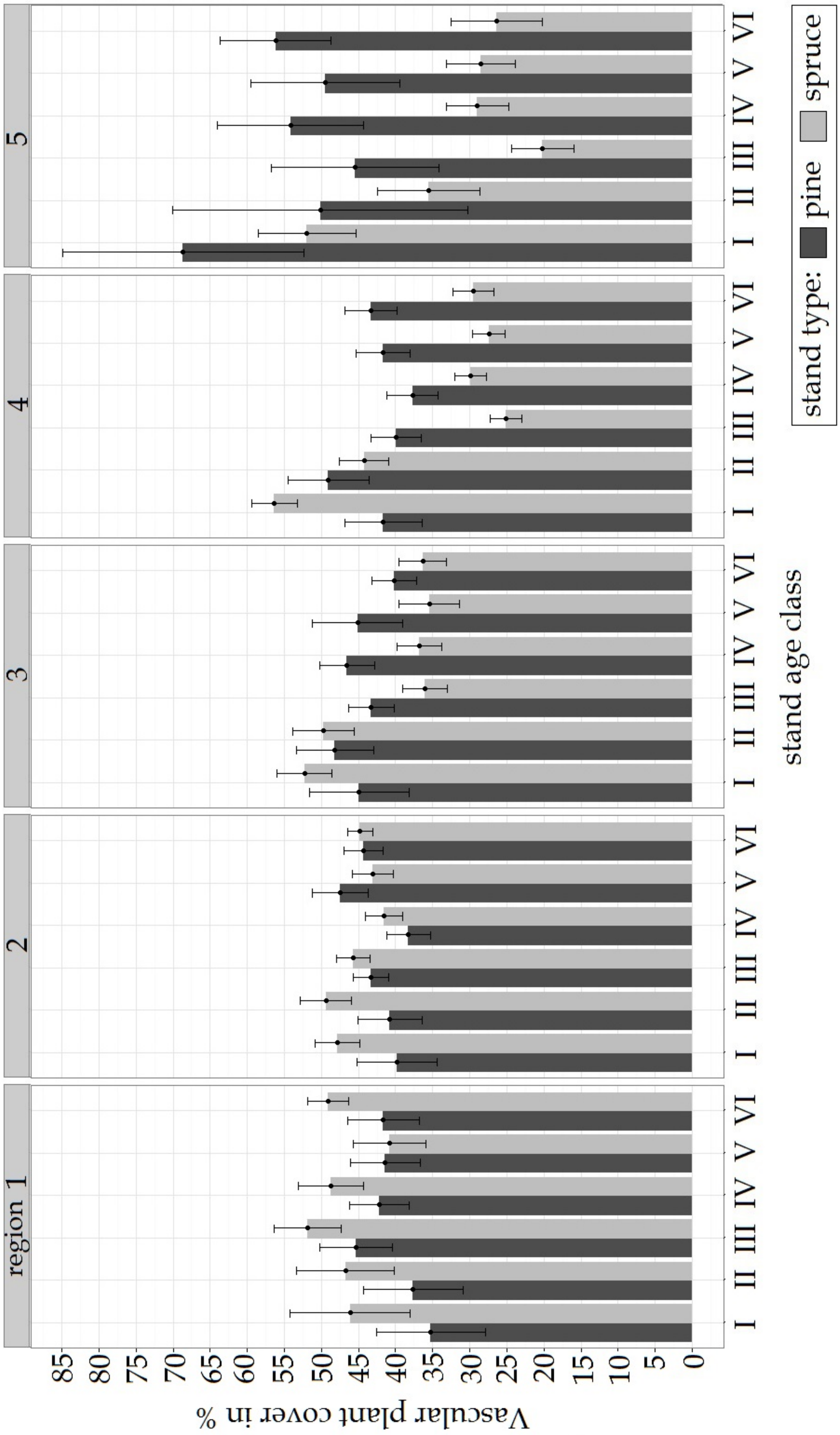

Figure 8. Vascular plant cover in % in the field-layer as an indicator of game potential dependent on stand type, age class (Table 1.) and region (Figure 3.) with 95% confidence intervals.

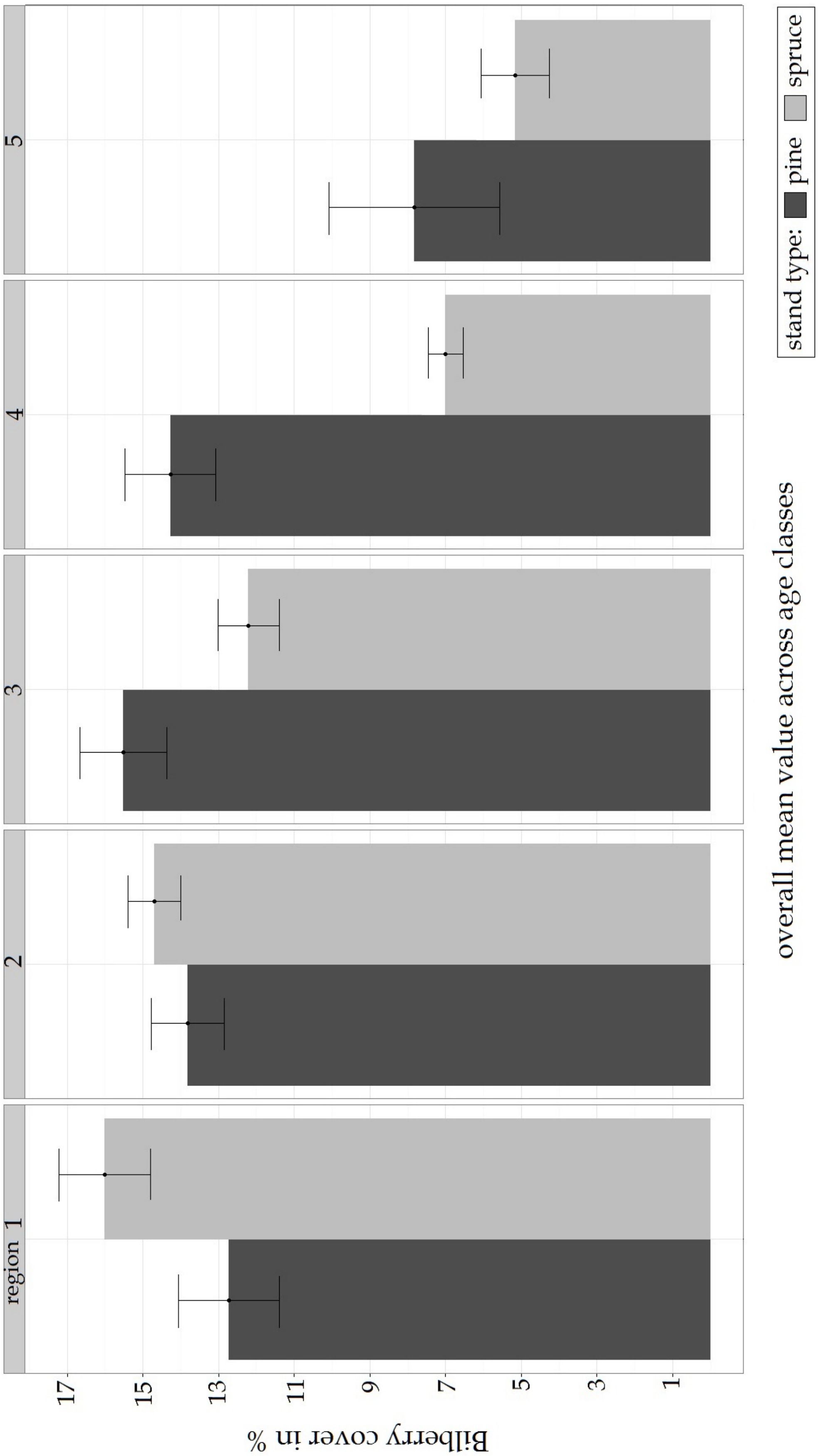

Figure 9. Overall mean values (across age classes) for bilberry cover in % dependent on stand type and region (Figure 3.) with 95% confidence intervals.

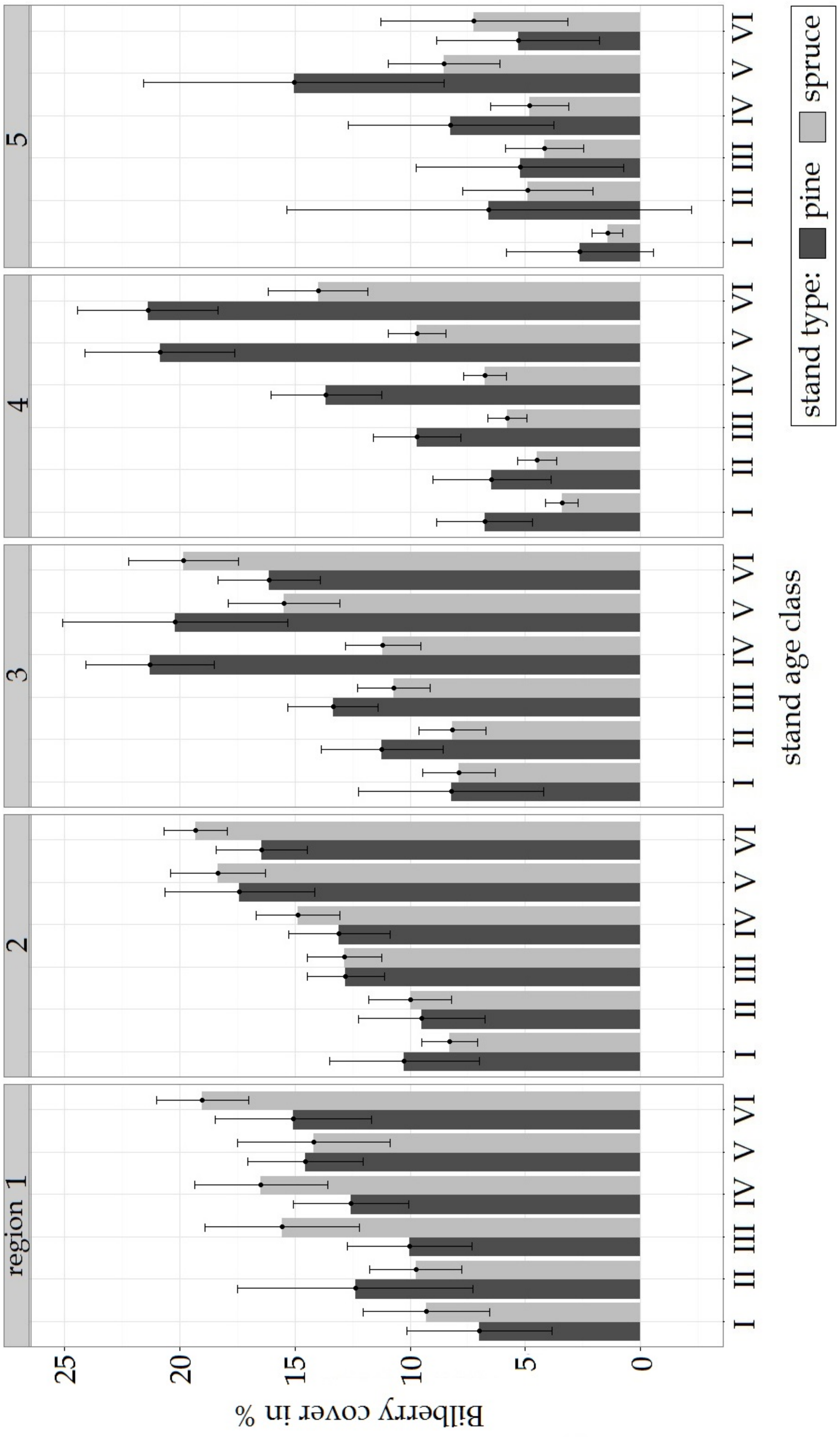

Figure 10. Bilberry cover in % dependent on stand type, age class (Table 1.) and region (Figure 3.) with 95% confidence intervals.

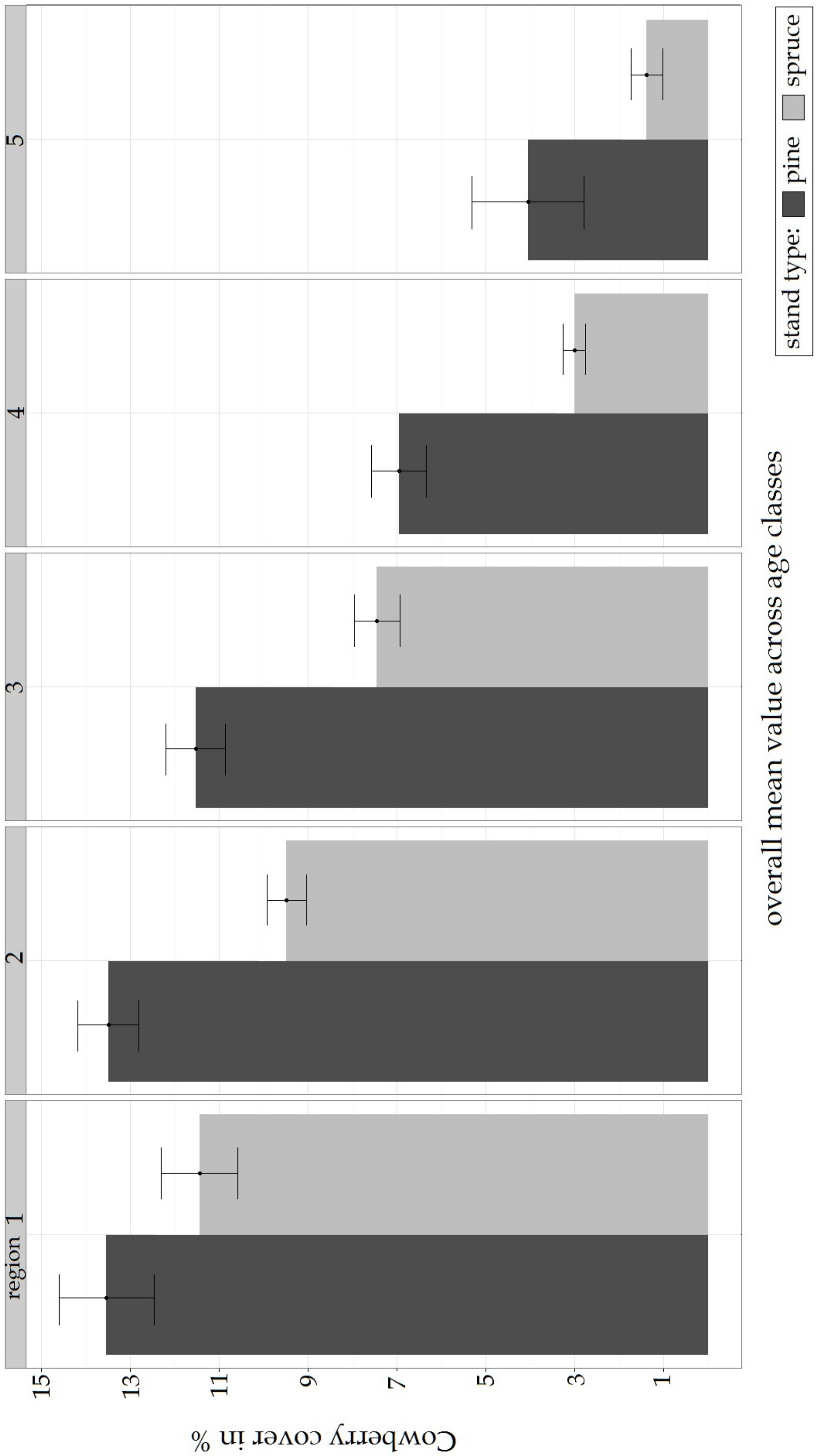

Figure 11. Overall mean values (across age classes) for cowberry cover in % dependent on stand type and region (Figure 3.) with 95% confidence intervals.

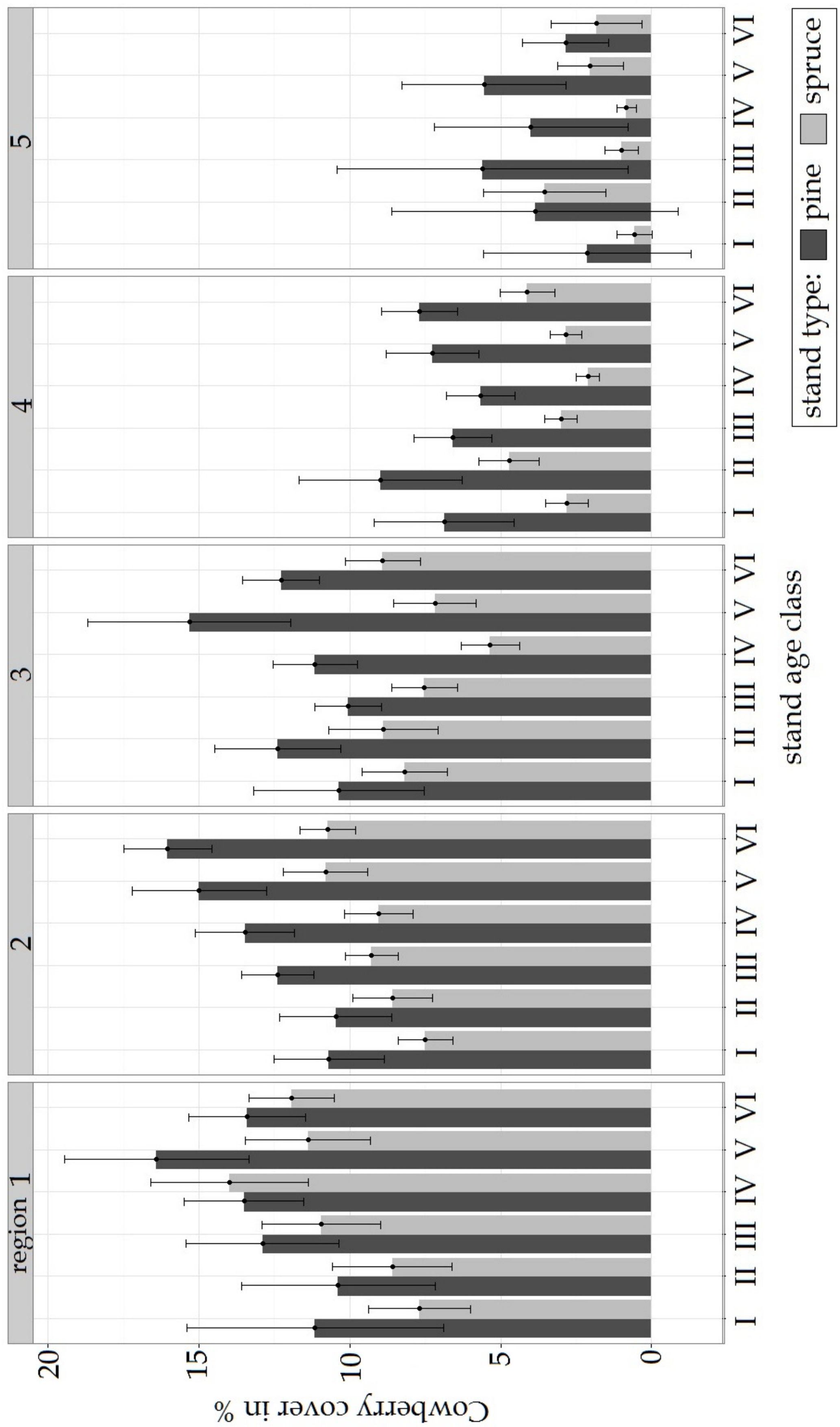

Figure 12. Cowberry cover in % dependent on stand type, age class (Table 1.) and region (Figure 3.) with 95% confidence intervals.

Discussion

This study shows that by analysing the NFI data and indicators there is great opportunity to increase our knowledge about the output of different ecosystem services depending on forest types, age distribution and management.

The results of the study supported hypothesis no. 1. According to these the potential for berry production increases proportionally to stand age, with the culmination in 5^{th} and 6^{th} age classes (from 70 to 100+ years old), both bilberry and most of cowberry cases. The same conclusion has been found in two different articles, which showed that an increase in forest age has a positive effect on berries species abundance (Kardell, 1980; Hedwall et al., 2013). In the latter study bilberry abundance increased with increasing forest age up to 80-100 year of age (Hedwall et al., 2013).

To study this provisioning ecosystem service the cover of bilberry and cowberry on the plot level was used as an indicator of berry production, although this is an indirect estimate. Previous studies have shown a strong positive relationship between the cover of these plants and the amount of berries produced (Turtiainen et al. 2011).

Figure 13. Light-open, transparent pine dominated stand with abundant understory vascular plants vegetation, in particular bilberry (photo: Daniel Boczniewicz).

Figure 14. Intermediate light-open spruce dominated stand with an abundant moss cover but very little vascular plants (photo: Daniel Boczniewicz).

The conducted analysis lends support to hypothesis no. 2 for cowberry, which has the best production output in pine dominated stands. In bilberry this hypothesis was only partially confirmed – a better production is observed in spruce dominated stands in northern part of Sweden (region 1-2), but in pine dominated stands in southern Sweden (region 3-5).

The berry shrubs need different condition for growth. Cowberry is most competitive on less fertile sites, while bilberry prefers higher nutrient availability. Pine is better adapted to poor site conditions, and more often planted on this site type, which may be one reason why the cowberry can be observed more often in pine dominated stands. Cowberry which is a more light-demanding species than bilberry has lower berry production in dense and overgrown stands in southern regions, comparing to northern ones.

The bilberry location in Sweden needs more explanation. This species deals better on more fertile sites, as the spruce – it is why spruce dominated stands in northern regions (1 and 2) host more bilberry shrubs. However in region 3 situation starts to change to convert completely in southern regions (4 and 5) for favour of pine dominated stands. Explanation of this situation is the site fertility change. Moving from northern to southern Sweden there is increase of soil fertility. According to this there are different conditions in the same stand types in region 5 and 1. The growth of pine and spruce dominated stands are much higher in southern Sweden as in northern one. In consequence the spruce dominated stands in southern Sweden grow much faster and the density inside the forest (especially in younger age classes) is much higher. Due to this there is much lower light availability and stands are really dark. In this situation the bilberry, which is sensitive for light changes (Hedwall et al., 2013) performed worst and the berry production decreases. In southern Sweden, pine dominated stands may be located on sites with appropriate fertility for bilberry with less dense overgrowth than in spruce stands. Due to this the bilberry shrubs start to occur in pine dominated stands due to better light availability and fertile site condition (Figure 13., 14. and 15.). Therefore, the set-up of this study limits the inferences, which can be made on the differences between the tree species. The really affecting factor for berry shrubs development is site index and light availability and the pine and spruce species can be indicators of this condition.

However, similar results can be found in other studies that also take site fertility into account. According to Gamfeldt et al. (2013) and Miina et al. (2009) there is a strong positive relationship between bilberry production and pine tree biomass. However in case of spruce the same authors observed a negative relationship. Different studies show, that coniferous stands promote berry species: there is an almost linear negative relationship between shrubs abundance and the volume of broadleaved tree species (Hedwall et al., 2013). However, too intense coniferous management can also decrease berry production – with increasing spruce volume up to 200-300 m^3 ha^{-1} there is a decrease of berry shrubs abundance (Hedwall et al., 2013).

Figure 15. Closed, dense spruce dominated stand without understory vascular plant vegetation (photo: Daniel Boczniewicz).

Based on this study some adaptations of forest management, which will promote berry species, may be suggested. Increasing forest age (rotation period) is significant, due to long time of recovery after disturbances as fire or clear-felling. Clear-cutting is considered to be negative for dwarf shrubs, especially bilberry (Kardell, 1980). An intensified thinning practice and favouring of pine species with open crowns will allow that more light reaches the understory and favours ground vegetation. However these management practices will impact negatively timber production (Nilsson et al., 2010). Therefore it is important to find a balanced combination between timber production and conservation of understory.

Also hypothesis no. 3 is supported. In the younger age classes a significant increase of biodiversity is observed – the number of vascular plant species in the field-layer grows up to reach its culmination in 2nd and 3rd age classes (from 10 to 39 years old). After culmination point there is observed decrease of biodiversity, due to fall of vascular plant species number in the field-layer with the lowest values in 5th and 6th age classes. According to this study after culmination of biodiversity growth in younger stages, there is visible decrease of this value, proportionally to increase of stand age. It seems to be true that biodiversity decreases with stand age, but this hypothesis fits better for southern region. In every plant succession the number of species, hosted by the environment can be grouped in three stages: increasing number of species – colonization of disturbed habitat, culmination of species richness and decrease. When the growing space is occupied, then competition starts and competitive species displace weaker ones. A very important factor, which facilitates this process is the fact that there are much more light-demanding than shade-tolerant vascular plant species. Due to higher soil fertility and more conductive climate, this process is faster in southern Sweden.

However these results can differ due to species, which are considered. For example mosses *Mnium hornum* and *Brachythecium rutabulum* colonise damp deadwood and they occur in old stands, where they can find such a conditions for growth (Meier et al., 2005). That is, while vascular plants, the species group targeted in this study, decrease with forest age, other species may increase.

This study describes vascular plant biodiversity in the field-layer in monoculture coniferous stands. Considering that different tree species are strongly related to different services, to use full potential of several economically, ecologically and culturally valuable ecosystem services we should move towards multi-species management and uneven-aged stands (Gamfeldt et al., 2013). Hence, it is really interesting to see that spruce forest seem to consistently host more species than pine throughout the rotation.

Hypothesis no. 4 is only partly supported. To study this supporting ecosystem service there were analysed cover of vascular plants on the sample plots. If the cover of vascular plants in the field-layer on the plot is high (no matters of species richness), it will encourage ungulates to stay in this stand, due to high level of fodder. It increases number of ungulates in that region and creating satisfactory level of game potential, which is directly connected with cultural ecosystem service.

Results vary due to regions and it is not easy to present explicit pattern. In southern regions (5 and 4) we can observed that there is higher game potential in younger and older stands in comparison with middle aged one for both coniferous species. Due to more fertile site condition there is fast vegetation development in younger stages and vascular plant cover is growing till moment, when stands start to be dense and light condition starts to be worse. It happens around middle aged classes and vascular plant cover is getting lower. After this situation there is thinning observed (natural or planned one) and stands starts to be light-open again. Then we can notice that vascular plant cover is increasing again. This scheme describes just really fertile sites in southern regions. Situation changes when we move to the north. Due to latitude climate change (from hemi-boreal to boreal zone) there is slower development of the vegetation. It means that in region 5 the first thinning can take place in 1st age class, when in region 1 it will be in 3rd age class (for the same spruce dominated stands in both cases). According to this we can conclude that vascular plants cover needs more time to develop in northern regions and differences between age classes will be not as visible as in southern regions.

There is also north-south gradient, which shows that higher game potential in northern region 1-2 is seen in spruce dominated stands, when for southern region 4-5 in pine dominated stands. The reason of this is similar as in berry production case – fertility and site index of region.

The hypothesis no. 5 is supported by this study. Differences between age classes in output of ecosystem services are much smaller in northern Sweden than in the southern. There are a few important factors, which shape this situation. The outputs varies so much in southern Sweden due to higher site fertility (higher site index), the more mild and friendly climate, the longer vegetation period and the better condition to growth. Due to this the overstory dynamics are faster and the rotation period is shorter in southern Sweden. Furthermore the forest in southern Sweden achieves full tree canopy closure, while stands in northern Sweden do not. In connection to this difference the variation in light conditions are in total larger in the south – there are stages from open till closed canopy, when in the north there is much more open ones. This factor has also significant influence for differences between age classes in output of ecosystem services, clearly visible in southern Sweden.

To summarize the influence of overstory (top canopy layer) for the understory ecosystem services (the bottom field-layer) I would suggest to divide Sweden for two regions: northern and southern.

In northern Sweden (especially regions from 1 to 3) there is really strong site index effect, which cannot be affected by management. Due to low site index and poor soil conditions the vegetation development is slow and we cannot observe closed canopy in spruce or pine dominated stands. Because of this we cannot shape overstory layer, so there is no possibility to mould understory. The suggestion for northern regions is prolongation of rotation period for promotion of berry production.

From the other hand in southern Sweden (especially region 5) we can observe tree species effects. Due to really high site index and soil fertility there is possibility to plant more pine or even introduce different tree species (as broadleaves), which will have better light condition for berry production, game forage potential and host higher vascular plants biodiversity.

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